

Antecedent snow conditions affect water levels and plant biomass of a fen in the southern boreal forest: results from an experiment using mesocosms

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Biogeochemical processes in peatland environments, such as carbon sequestration and decomposition, are affected by variation in water supply. Across the boreal forest biome, climate change threatens to either alter rates of annual precipitation or skew the timing and ratio of rainfall and snowfall events. To simulate moisture variability during the ice-free season, cylindrical mesocosms (diameter 1.5 m) were installed in a southern boreal patterned fen in central Saskatchewan, Canada, to enable manipulations of antecedent snow conditions. The objectives of the study were to assess the utility of *in situ* mesocosms for peatland ecohydrology research and to test for effects of snow manipulations on fen plant communities. After spring thaw, initial water depths were greatest and dates of surface water disappearance were latest in the snow addition mesocosms, followed by the control and snow removal mesocosms. In contrast, maximum frost levels and frost disappearance dates in the snow addition mesocosms were intermediate to those of the control and snow removal mesocosms. Densification of snow during snow manipulation events is suggested to account for this confounding outcome. Of the nine plant taxa identified in the harvests of aboveground biomass from all mesocosms, buckbean (*Menyanthes trifoliata*) biomass was most strongly related to variation in surface water conditions. Climate conditions that favour persistence of either herbaceous- or graminoid-dominated communities will likely affect the carbon storage function of southern boreal fens.

Introduction

For many ecosystems, general increases in mean annual temperatures due to climate warming are of secondary importance compared with changes

to precipitation regimes and watershed hydrology (Vitousek 1994, Tilman 1998). The carbon dynamics of boreal peatlands are tightly coupled to variation in water supply (Bubier 1995, Weltzin *et al.* 2003) and seasonal frost depth

and duration (Woo and Winter 1993). For millennia, peatlands have functioned as reservoirs of sequestered carbon derived from atmospheric carbon dioxide (Gorham 1991). With the advent of climate warming, this ecosystem function is threatened (Carroll and Crill 1997, Price *et al.* 1999).

Peatlands that occur within transition zones between major ecoregions are forecast to be particularly vulnerable to climate warming (Gignac *et al.* 1998). The southern boreal forest (or "boreal fringe") of western Canada exists between the boreal forest and prairie aspen parkland ecoregions, where the southern extent of the forest-grassland boundary is determined by chronic moisture deficits (Hogg 1997). Among the most common peatland forms that occur within this zone are fens and bogs. The hydrologic dynamics of fens, in particular, are strongly affected by surface and groundwater flow. Patterned (also known as "ribbed") fens are characterized by a mosaic of distinct wet peaty depressions ("flarks") and drier ridges ("strings") that are perpendicular to the direction of water flow (Zoltai *et al.* 1988). Interactions between water supply and peat density affect specific water levels within fens yielding a distribution of flarks that ranges from areas where the water table is subsurface (water level < peat surface) to surface pools (water level > peat surface).

Temporal variation in peat hydrology occurs seasonally and annually (Quinton and Roulet 1998). In the southern boreal forest, within years, net water levels tend to drop during ice-free months following initial springtime recharge from snowmelt. Among years, the roughly decadal wet-dry cycle (or "oscillating water-level fluctuations") encompassing successive years of abundant rainfall and prolonged drought accounts for longer-term patterns of variation in water levels (van der Valk 2005). Superimposed on these more cyclical sources of temporal variation is the directional influence of climate warming. For the southern boreal forest, climate warming is forecast to reduce annual rates of precipitation and alter the phenology of fall frosts and spring snow melts (Moore *et al.* 1998), which may, in turn, affect the annual CO₂ balance of peatlands (Aurela *et al.* 2004). Such overlapping temporal dynamics make recognition of the impacts of

climate change on peatland ecosystems under natural conditions challenging.

Characterization of peatland vegetation under manipulated hydrologic conditions represents one option for forecasting ecosystem-level responses to climate variability. Plant community structure is strongly affected by peat hydrology (Camill 1999), as some groups of plants are adapted to short-term hydrologic variation and others are adapted to prolonged periods of relative wetness or dryness (Weltzin *et al.* 2003). Herbaceous wetland plants, for example, may be useful integrators of short-term hydrologic variation as they can exhibit growth rates within a season that vary according to the presence and duration of standing waters in peatlands. Similarly, along hydrologic gradients, biomass distributions among plant species may be useful to forecast changes to community structure under various climate change scenarios (Thormann *et al.* 1998).

Practical field methods are needed to test specific hypotheses of the consequences of climate warming on the ecohydrology of these systems. Traditionally, peatlands have either been studied under ambient conditions (i.e. field observations and measurements) or under laboratory conditions using extracted peat monoliths. *In situ* mesocosms (or enclosures) have long been used to manipulate environmental factors in aquatic environments under semi-natural conditions (e.g. Frost *et al.* 1988). However, it is unknown if similar techniques are suitable for semi-aquatic environments such as bogs and fens. The objectives of this study were to: (1) assess the utility of mesocosms in fen environments to manipulate hydrologic variation, and (2) quantify the effects of altered water and frost levels on plant communities.

In this field study, mesocosms were used to isolate peat monoliths to estimate the effects of variation in antecedent snow pack conditions during the winter on peat hydrology during the spring and summer. Properties of snow cover are related to the thermal and hydrologic regimes of peatland soils (Granberg *et al.* 1999). The physical and temporal aspects of peat hydrology that were investigated in this study as a function of snow pack included above peat surface water depths and subsurface depths to frost, and

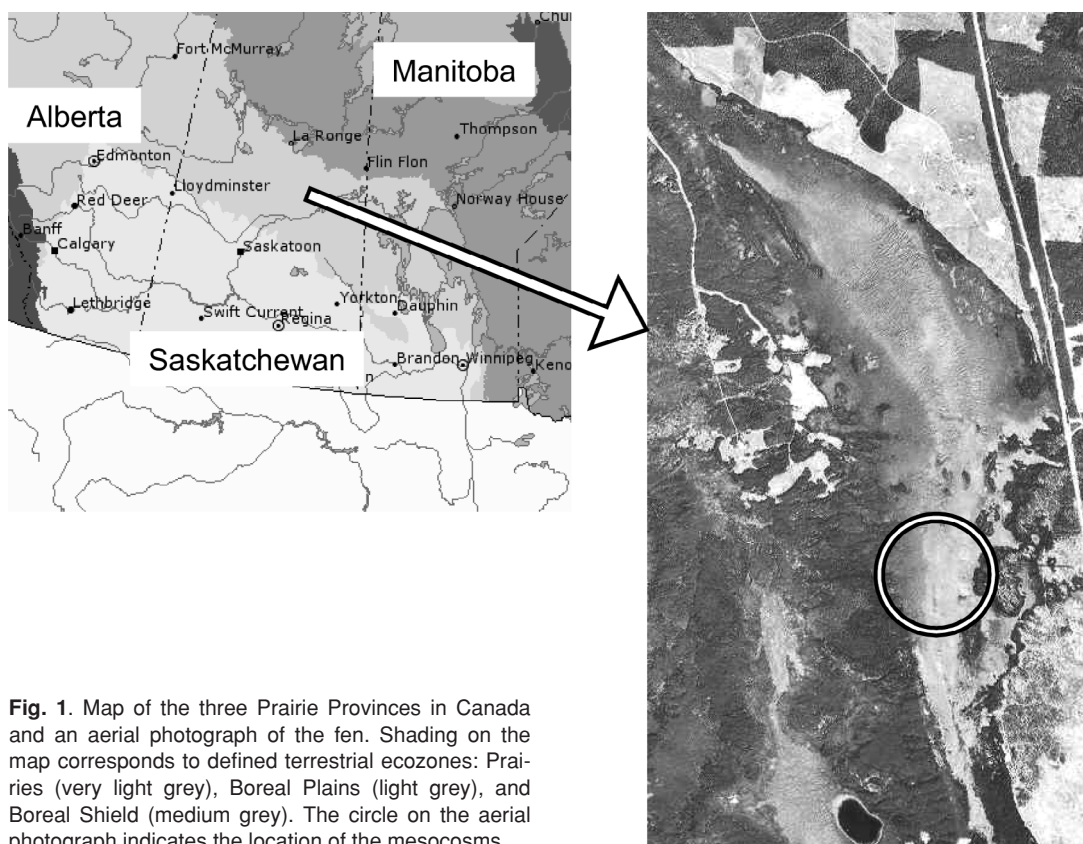


Fig. 1. Map of the three Prairie Provinces in Canada and an aerial photograph of the fen. Shading on the map corresponds to defined terrestrial ecozones: Prairies (very light grey), Boreal Plains (light grey), and Boreal Shield (medium grey). The circle on the aerial photograph indicates the location of the mesocosms.

disappearance dates of surface waters and sub-surface frosts. Further, aboveground vegetation from each mesocosm was harvested at the end of the summer to estimate the effects of the snow manipulations on plant community structure. The general applicability of using field mesocosms in peatland ecosystems for simulating scenarios of climate warming is also discussed.

Study site

The fen used in this study was located in the White Gull Creek watershed of the boreal fringe approximately 40 km north of Smeaton, Saskatchewan, Canada ($53^{\circ}46'N$, $104^{\circ}36'W$), just north of the prairie parkland ecozone, and it is typical of the transitional mid-boreal region (Zoltai *et al.* 1988). The fen is approximately 4000 m (N–S) by 450 m (E–W), with a 0.1% gradient that slopes from north to south (Fig. 1). This peatland was originally used as one of

the BOREAS (Boreal Ecosystem–Atmosphere Study) sites (SSA — Southern Study Area) and is currently a member site of BERMS (Boreal Ecosystem Research and Monitoring Sites) and Fluxnet Canada. The dominant upland forest species surrounding the fen include black spruce (*Picea mariana*) and tamarack (*Larix laricina*). Mean summer and winter temperatures are $14^{\circ}C$ and $-13.5^{\circ}C$, respectively. Mean annual precipitation is approximately 500 mm, as is mean annual evapotranspiration (Nijssen and Lettenmaier 2002). Peat depths within the fen range from <1 m at the edges to ~ 3 m near the centre (Rask *et al.* 2002).

The proportion of the fen covered by surface waters varies over time, corresponding to climatic oscillations that yield a roughly decadal wet-dry cycle (Diaz 1986). In May 1994, much of the fen was covered by shallow water (Rask *et al.* 2002). By March 2001, only the western edge of the fen had pools or small ponds. Groundwater is a major source of water to the fen, supple-



Fig. 2. Photo of a single flark with snow addition, control and snow removal mesocosms. A snow removal mesocosm is shown in the foreground.

mented by snowmelt and periodic rains. Surface flow in recent years has been restricted to the spring, when frost inhibits infiltration of snowmelt waters. However, prior to frost break, the peat is typically saturated to the surface. Water samples from surface pools during 2002 and 2003 had pH from 7.3 to 8.0, alkalinity from 34 to 81 $\mu\text{g l}^{-1}$ and dissolved organic carbon from 14.8 to 28.1 mg l^{-1} . Towards the end of the growing season during each of 2002 and 2003, the water table dropped to depths greater than 30 cm below the surface of the peat (Hogan 2006).

Materials and methods

Eighteen cylindrical mesocosms were installed across six flarks in mid-October 2002, before any autumn freezing of peat occurred (Fig. 2). The mesocosms were made of 3.175 mm sheets of white low-density polyethylene. Mesocosms were 1.524 m in diameter by 0.914 m in height, and were bottomless. At each flark, three mesocosms were pounded into the peat until they were approximately two-thirds buried (~ 70 cm below the peat surface).

The three mesocosms were assigned to one of three treatment levels (snow addition, snow removal, or control). In addition, reference locations were established in open fen areas outside

of the mesocosms as a check on how well the control mesocosms mimicked natural conditions. After the mesocosms were installed, boardwalks were laid to facilitate easy access to the mesocosms and to reduce disturbance to the surrounding flark areas. Four posts were driven into the peat immediately outside each of the mesocosms to serve as supports for orange snow fencing which was used to contain added snow that exceeded the height of the mesocosms above the peat surface (i.e. $> 20\text{--}30$ cm).

Snow manipulations were conducted based on data from bimonthly snow surveys (Meteorological Service of Canada) and snowfall accumulation as measured by a Belfort gauge. On average, snow was manipulated once every two to three weeks, from late December 2002 until early March 2003. Using plastic shovels, snow was either added to or removed from two of the three mesocosms at each flark on each occasion. Initial surveys in mid-December indicated that snow depth across the fen was approximately 20 cm. On snow manipulation occasions, snow depth was reduced by 15–20 cm total depth for the snow removal mesocosms and increased by approximately 10 cm at the snow addition mesocosms. No snow manipulations occurred at the control mesocosms or the open fen areas.

Following spring thaw, the study area was surveyed once every seven to ten days, starting

on 2 May 2003, for a maximum of 18 surveys. Water and frost levels were recorded relative to the peat surface in the mesocosms and the open fen areas using a graduated metal probe. Three measurements were taken from the central portion of each mesocosm (i.e., > 20 cm from the edge). Water levels were measured from the surface of the water to the peat surface and they were recorded until water levels dropped below the peat surface. Frost levels were measured from the peat surface to the depth at which the frost probe ceased penetration in the peat and they were recorded until the frost probe penetrated the peat without resistance.

At the end of August, all aboveground vegetation from each of the mesocosms was harvested. Snips were used to cut plants as close to the surface of the peat as possible. Plant material was stored in a cooler and transported to laboratory facilities in Saskatoon where samples were processed within two days. Plants were sorted into taxonomic groups and initial wet weights were recorded. The plants were then dried at 80 °C for 72 h, so that dry weights could be recorded and water content calculated.

Analysis of variance (ANOVA) was used to estimate the influence of antecedent snow conditions on peat hydrology. There were two sets of dependent variables that described variation in water and frost levels: initial water depth and final frost level, and date of disappearance of surface water or frost. Dunnett's test (one-tailed) was used to compare water and frost levels in snow addition and snow removal mesocosms to control mesocosms. ANOVA was also used to test for differences in total aboveground vegetation biomass and by major taxonomic groups as a function of snow manipulation treatment levels. Tukey's Honest Significant Difference (HSD) test were used to test for differences between treatment levels. All statistical analyses were performed using SAS, version 8 (SAS Institute Inc., Cary, North Carolina).

Results

By the end of the period of snow manipulations, total snow depth increased steadily until it was approximately 40 cm at the control mesocosms.

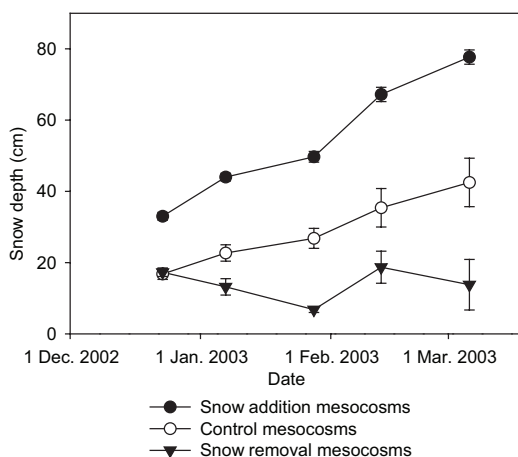


Fig. 3. Results of snow manipulations applied to the mesocosms from late December 2002 until early March 2003. Snow addition values are sums of the base snow encountered and the amount of snow added on each snow manipulation occasion. Error bars are standard deviations. Snow removal values are prior to clearing, or the depth of snow that fell between each manipulation occasion. Each data point is an average over all six mesocosms.

The combination of natural snow accretion and snow addition manipulations yielded almost 80 cm total snow depth in the snow addition mesocosms (Fig. 3). These snow manipulations significantly altered snow depths across treatment levels by the end of the snow manipulation period (ANOVA: $F_{2,15} = 182.7$, $P < 0.0001$).

Two months after the snow manipulations ceased, all of the snow addition and control mesocosms and open fen areas had standing water (Fig. 4). Only half of the snow removal mesocosms (three of six flarks) had standing water. Frost was encountered, between depths of 15 and 25 cm below the peat surface, in all mesocosms and open fen areas. Between 11 July and 23 July, surface waters disappeared from all of the mesocosms and open fen areas (Table 1). During the same time, frost disappeared from the snow addition and control mesocosms, but it did not disappear from the last of the snow removal mesocosms until the last week of August. Frost disappeared most rapidly from the open fen areas, where all frost was absent by the first week of July.

Initial water depths were greatest in the snow addition mesocosms (mean = 22.7 cm) and least

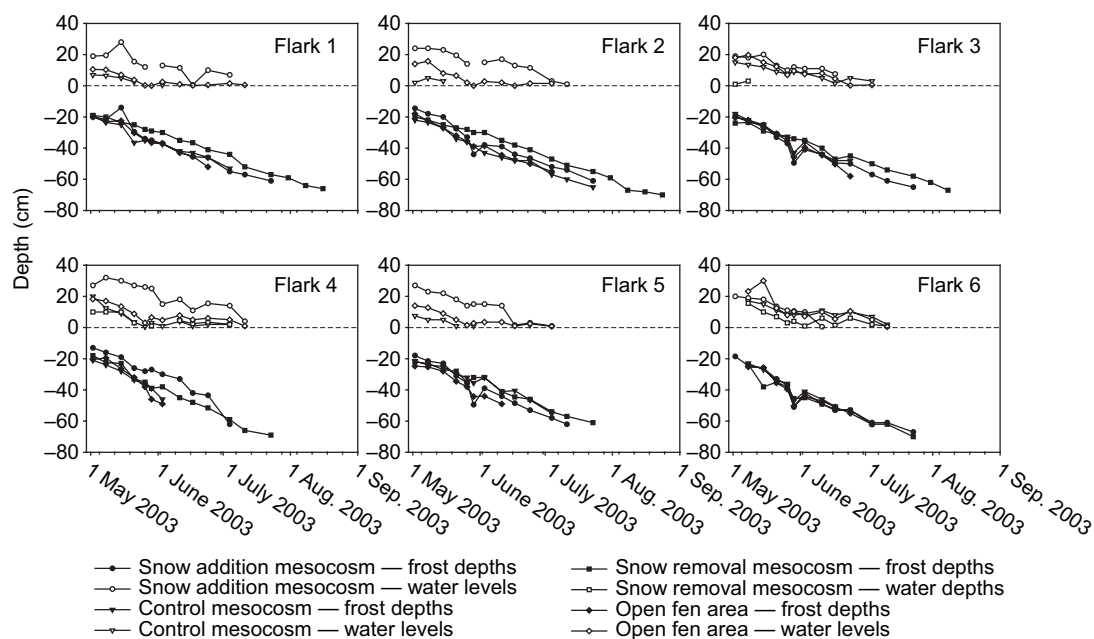


Fig. 4. Time series plots of water levels and frost depths for all mesocosms and open fen areas within each of the six flarks.

in the snow removal mesocosms (mean = 5.0 cm); control mesocosms and open fen areas had intermediate depths (Fig. 5). On the dates when frost disappeared, frost levels were greatest in the snow removal mesocosms and least in the open fen areas. Frost levels in snow addition mesocosms (mean = 63.0 cm) were almost

as great as those in snow removal mesocosms (mean = 67.2 cm) and control mesocosms (mean = 52.9) had frost levels only slightly greater than those in open fen areas (mean = 50.8 cm).

Frost levels differed significantly among mesocosm treatment levels both by date and by depth (Table 2). Water levels also significantly

Table 1. Summary statistics for water and frost measurements by date and by depth. "Earliest date", "Mean date" and "Latest date" for treatment levels associated with Water and Frost headings refer to the dates when surface water and frost, respectively, disappeared from the mesocosms and open fen areas. The Water heading "Mean depth" refers to the initial depth of water in the mesocosms or open fen areas; these depths were all recorded on 2 May 2003. The Frost heading "Mean depth" refers to the maximum depth at which frost was detected in the mesocosms or open fen areas; these depths varied by date.

	Disappearance dates			Mean depth (cm)
	Earliest date	Mean date	Latest date	
Water				
Snow addition	11 June	8 July	11 July	22.7
Control	15 May	23 June	11 July	11.6
Snow removal	1 May	29 May	11 July	5.0
Open fen	22 June	6 July	7 July	16.6
Frost				
Snow addition	4 July	17 July	23 July	63.0
Control	3 June	27 June	23 July	52.9
Snow removal	23 June	4 August	24 August	67.2
Open fen	7 June	17 June	25 June	50.8

differed among mesocosm treatment levels by depth. Significance was not obtained for differences in water levels by date among mesocosm treatment levels, though the pattern was similar. No differences in water and frost levels were obtained for specific comparisons between mesocosm controls and open fen areas by date or by depth.

A total of nine taxonomic groups of plants were identified across all mesocosms (Table 3). One of the groups, graminoids, included at least four species of sedges and grasses common to the region (Johnson *et al.* 1995). Across the taxonomic groups, only buckbean and graminoids occurred in all three mesocosms in every flark. Together, these two groups comprised greater than 95% of both the total wet and dry weight biomasses of all plants combined. For total wet biomass, buckbean and graminoids accounted for 57% and 41%, respectively, and for total dry biomass, buckbean and graminoids accounted for 41% and 56%, respectively.

Table 2. One-way ANOVAs for the effects of mesocosm treatment levels (snow addition, control, snow removal) and comparisons between control mesocosms and open fen areas on water and frost dates of disappearance, and initial water depths (2 May 2003) and final frost depths. For the mesocosm treatment comparisons, $n = 6$ and d.f. = 2,15. For the control mesocosm and open fen comparisons, $n = 6$ and d.f. = 1,10. Dunnett's tests refer to significant differences ($* = P < 0.05$) between snow addition or snow removal mesocosms and snow control mesocosms. n.s. = not significant.

	ANOVAs		Dunnett's test	
	<i>F</i>	<i>P</i>	Snow addition	Snow removal
Mesocosm treatment levels				
Water				
Date	3.13	0.073	n.s.	n.s.
Depth	11.24	0.001	Deeper*	Shallower*
Frost				
Date	11.35	0.001	Later*	Later*
Depth	15.24	< 0.001	Deeper*	Deeper*
Open fen and control comparisons				
Water				
Date	1.51	0.248		
Depth	2.01	0.187		
Frost				
Date	1.99	0.189		
Depth	0.33	0.581		

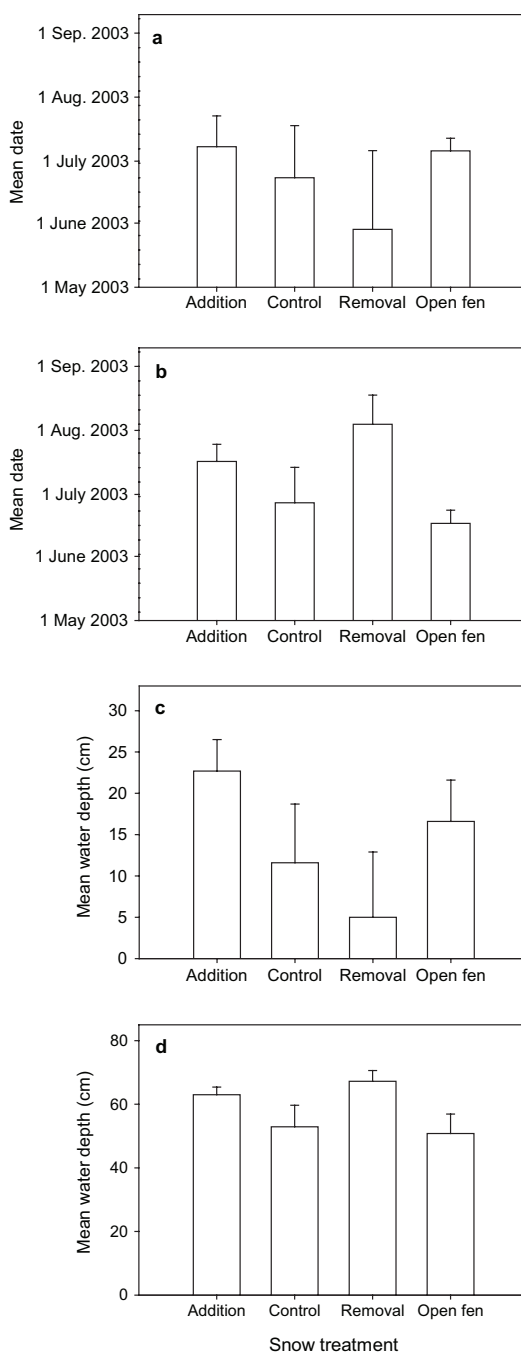


Fig. 5. Comparisons of mean disappearance dates (**a**, **b**) and depths (**c**, **d**) for water and frost depths among mesocosms. Error bars are standard deviations. **a:** Mean disappearance dates of standing water. **b:** Mean disappearance dates of frost. **c:** Mean initial water depths. **d:** Mean maximum final frost depths.

Table 3. Mean wet and dry weights (and standard deviations) for aboveground vegetation among mesocosms according to treatment level (snow addition, control, and snow removal). Mesocosm occupancy refers to the number of mesocosms per treatment level in which a particular taxa was found (maximum = 6).

Name	Mesocosm occupancy (A, C, R)	Wet weights (g)			Dry weights (g)		
		Snow addition	Control	Snow removal	Snow addition	Control	Snow removal
Buckbean (<i>Menyanthes trifoliata</i>)	6, 6, 6	448.0 ± 71.7	240.2 ± 100.1	159.3 ± 75.6	93.5 ± 17.5	51.2 ± 22.5	34.2 ± 15.7
Graminoids (<i>Carex</i> -dominated) ^a	6, 6, 6	196.6 ± 59.6	181.5 ± 90.9	200.2 ± 87.9	81.0 ± 21.9	73.3 ± 33.7	89.2 ± 48.8
Bog willow (<i>Salix pedicellaris</i>)	3, 2, 3	1.8 ± 1.1	9.3 ± 8.6	4.9 ± 5.8	0.8 ± 0.5	4.6 ± 4.9	1.6 ± 1.7
Dwarf bog-rosemary (<i>Andromeda polifolia</i>)	2, 2, 1	2.1 ± 2.6	2.7 ± 1.6	0.1	0.6 ± 0.7	0.8 ± 0.6	0
Scouring rush (<i>Equisetum hyemale</i>)	2, 0, 2	1.4 ± 1.4	0	3.3 ± 0.3	0.3 ± 0.3	0	0.9 ± 0.2
Knotted rush (<i>Juncus nodosum</i>)	0, 2, 1	0	63.8 ± 36.3	28.3	0	19.5 ± 11.9	8.6
Cattail (<i>Typha latifolia</i>)	0, 2, 0	0	3.6 ± 0.5	0	0	1.0 ± 0.2	0
Rough-leaved rice grass (<i>Oryzopsis asprifolia</i>)	0, 1, 0	0	75.2	0	0	19.7	0
Dwarf birch (<i>Betula glandulifera</i>)	0, 0, 1	0	0	3.2	0	0	0.9
Richness (# taxa)		5	7	6	5	7	6

^a Graminoids primarily included bog sedge (*Carex interior*), inland sedge (*Carex capillaris*), and tall cotton grass (*Eriophorum angustifolium*).

When all plants were combined, wet weights significantly differed among treatments; dry weights did not (Table 4 and Fig. 6a). For buckbean alone, both wet weights and dry weights were significantly different among treatments (Fig. 6b). No significant differences were observed for any graminoid comparisons (Fig. 6c), nor did water content systematically vary with mesocosm treatment level among any of the taxonomic groups (Table 4). Water content was approximately 70% when all plants were combined across mesocosms, 79% for buckbean and 59% for graminoids. Post-hoc Tukey HSD test revealed that where significant differences occurred, snow addition mesocosms differed from the snow removal and control mesocosms. Variation in buckbean biomass among treatments reflected snow manipulation effects on initial water levels and disappearance dates. Graminoid biomass was not statistically related to any of the water or frost measurements.

Discussion

The lack of statistical differences between control mesocosms and open fen areas indicates that the mesocosms performed acceptably well at simulating natural hydrologic conditions of peat during the year of the experiment. Relative differences between initial water depths and surface water disappearance dates are consistent with models of climatic variation involving greater or lesser rates of precipitation (Moore *et al.* 1998, Thormann *et al.* 1998). However, deeper final frost levels and later disappearance dates of frost observed in the snow addition mesocosms compared to the control mesocosms and open fen areas suggests that some attribute of the snow addition treatment affected the thermal properties of the isolated peat monoliths.

In theory, the presence and depth of snow provides insulation to the underlying peat by isolating it from colder atmospheric air temperatures (Moore 1987, Romanovsky and Osterkamp 2000). Through the use of a simulation model for boreal mixed mires and subsequent field validation, Granberg *et al.* (1999) found that a 25% decrease in precipitation during the winter prolonged the duration of frost by almost two

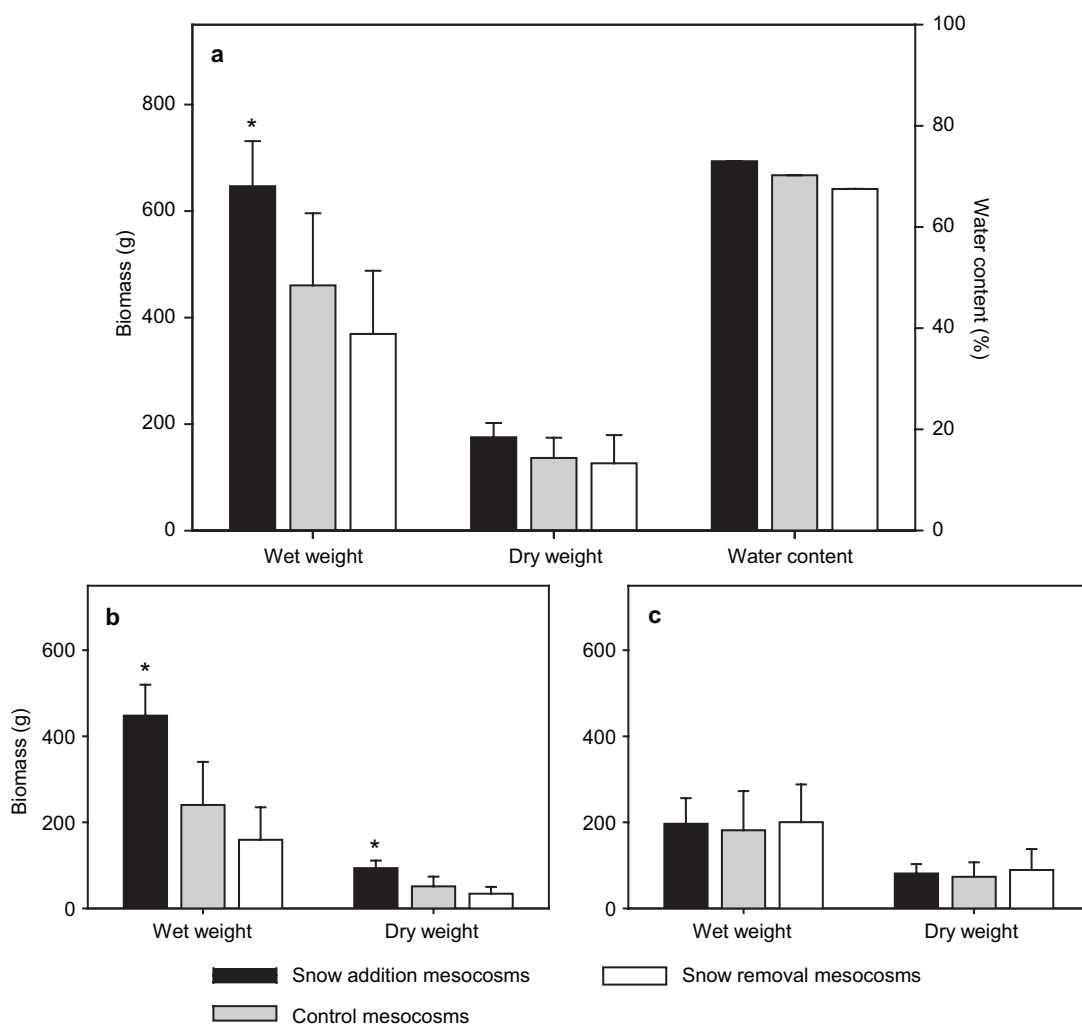


Fig. 6. Wet and dry biomass of aboveground vegetation harvested from snow manipulation mesocosms. Error bars are standard deviations and asterisks indicate treatment levels that are significantly different (Tukey HSD tests). **a:** All plants combined. **b:** Buckbean. **c:** Graminoids. In panel **a**, the right-hand axis is for water content only.

months. They also found that the period of frost was decreased by approximately one month when winter precipitation was doubled. The net effect was an earlier onset of thaw in the spring

and frost that was shallower and thinner. Similar results were obtained for simulation models of ground thermal regime near Barrow, Alaska, based on the timing and duration of seasonal

Table 4. One-way ANOVA for all plants combined, buckbean and graminoid responses to the snow manipulations. Total biomass includes all species listed in Table 3. For all comparisons, d.f. = 2,15.

Vegetation	Wet weights		Dry weights		Water content	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
All plants combined	4.90	0.02	2.67	0.10	1.65	0.23
Buckbean	19.13	< 0.0001	15.89	0.0002	0.44	0.65
Graminoids	0.09	0.91	0.28	0.76	0.26	0.77

snow cover (Ling and Zhang 2003).

The degree of thermal insulation provided by snow cover is at least partially dependent on the physical structure of the snow (Goodrich 1982, Sturm *et al.* 1997). Lighter snow with greater loft (i.e. less dense) provides more insulation than heavier and wetter snow (i.e. more dense) because a greater volume of the snow cover is comprised of interstitial air pockets. In our study, the process of heaping snow into the snow addition mesocosms may have had the opposite effect; it may not have insulated the peat from colder atmospheric temperatures. Densification of snow within the snow addition mesocosms likely made the snow cover more conductive of cold temperatures. The diminished thermal insulation in the snow addition mesocosms was not as severe as that in the snow removal mesocosms, which experienced the deepest frost levels and the latest disappearance dates of frost. This effect of densification may also have been exacerbated by compaction of snow surrounding the snow addition and removal mesocosms that resulted from accessing the mesocosms to either add or remove snow.

Maximum frost level (or depth to frost) specifically refers to the depth or thickness of the peat without frost from the surface; it does not indicate how thick the frost was. Frost thickness could only be estimated by assuming that the frost was relatively thin on the penultimate sampling occasion that preceded the final sampling occasion when frost disappeared. Estimation of frost thickness is less important than the depth to frost-free peat when studying the biogeochemistry or ecology of peatlands because the rates of these processes are greatly reduced under frozen conditions. In contrast, when considering the hydrology of peatlands, rates of subsurface flow below the frozen layer are partly dependent on the thickness of the frost, in combination with the composition of the substrate, and the underlying slope of the peatland basin (Kingsbury and Moore 1987).

The maximum depths to frost observed outside of the mesocosms, in the open fen areas, occurred at approximately 51 cm, and were not significantly different than those observed in the control mesocosms. These depths were 15–20 cm shallower (i.e. closer to the peat surface) than

the depth of the bottom edge of the mesocosms. Mean maximum frost levels in the snow addition and snow removal mesocosms were 63 cm and 67 cm, respectively. These levels approximately intersect the bottom edge of the mesocosms, suggesting that deeper mesocosms may have resulted in even greater depths to frost. Melting in the spring from below the frost has been shown to be more important than from above in a fen with a dry peat surface (Kingsbury and Moore 1987). The area of Sandhill Fen used for this study was supersaturated with water (i.e. the surface was pocked with ponds and pools 10–20 cm deep) when this experiment was initiated. Unlike a dry peat surface, where heat flow from the surface to the frozen peat is reduced by the presence of a boundary layer (FitzGibbon 1981), water saturation of the peat surface conducts heat more rapidly to greater depths. In addition, patterned fens, including the fen used in this study, are characterized by both vertical and lateral flow. Subsurface lateral flow during spring thaw was restricted within the mesocosms, meaning that heat and energy exchange was also restricted. Taken together, these observations suggest that frost thaw rates were likely greater from above than from below.

As compared with quadrat samplings from a series of transects established adjacent to the mesocosm study area in June 2003, aboveground biomass was approximately 70% that of open fen areas when both snow control mesocosms and quadrats were harvested in August (K. Gardiner and G. Benoy, Environment Canada unpubl. data). This decrease in biomass was similar for both wet and dry biomass of all plants combined and for buckbean and graminoids, the dominant taxonomic groups. Plant growth may have been impeded along the inside edge of the mesocosms due to disturbance to roots during mesocosm installation and reduced foliar exposure to sunlight due to shading from aboveground portions of the mesocosms. In addition, the presence of the mesocosms in the peat to a depth of 70–80 cm impeded lateral water flow throughout the study. Thus, nutrient supply and replenishment may have been reduced within the mesocosms. However, vegetation community structure was comparable between the snow control mesocosms and the quadrats, suggesting that any of

these potentially confounding effects did not differentially affect specific taxa.

That buckbean was the only plant species to exhibit significant differences among treatment levels as a result of the snow manipulations is not surprising as it is a species that is common to shallow surface waters (Johnson *et al.* 1995). In addition to graminoids, some of the other commonly identified plants were woody species, including bog willow and dwarf bog-rosemary. Although these woody plants may not have greatly altered rates of production within a single season, their presence in approximately half of the mesocosm in all treatments suggests that vegetation composition within each flark was relatively homogeneous at initiation of the experiment. Prolonged drawdown of water levels or inundation would likely be necessary to significantly alter the assemblage of bryophyte and woody vegetation (Camill 1999).

Patterns of buckbean biomass were consistent with the predicted effects of snow manipulations on initial water levels and water disappearance dates. Deeper initial water depths were strongly correlated to duration of standing water in snow addition mesocosms. Perennial herbaceous plants are adapted to take advantage of periodic inundations of flark habitats. However, high growth rates of aboveground herbaceous tissue during the growing season are countered by rapid decomposition rates that affect the proportion of carbon that can be retained in the ecosystem. In a field study of a patterned fen near Schefferville, northern Quebec, Moore (1989) found that buckbean lost 80% of its mass after three years, compared to loss of 25% to 35% for shoots of tufted bulrush (*Scirpus caespitosus*) and leaves of leatherleaf (*Chamaedaphne calyculata*). An accompanying carbon budget showed that carbon sequestration was about $40 \text{ g m}^{-2} \text{ yr}^{-1}$ at fen string sites dominated by bulrush and leatherleaf and approximately carbon neutral at the pool sites dominated by buckbean. Climatic conditions that result in prolonged periods of inundation may alter the carbon balance of fens by shifting community composition from graminoids and woody species to emergent and submergent aquatic species.

A major challenge of climate change science is the design of experiments that simulate forecasted climatic conditions. Field manipulations

represent one option for isolating putative properties of ecosystems that drive key biogeochemical and ecological processes (Bridgman *et al.* 1999, Groffman *et al.* 2001). By varying antecedent snow conditions among experimental mesocosms in this study, desired contrasts in water levels and surficial pool duration were obtained. In semi-aquatic environments, including peatlands, the success of snow manipulations is partially predicated on the prevailing water levels. For example, in a fen with relatively high water levels (i.e. submerged vegetation) in the fall, variation in snowpack would not likely matter when compared with antecedent hydrologic conditions.

Other studies that have examined effects of variation in snowpack on peatland ecosystems have done so primarily through the use of snow fencing (Scott and Rouse 1995, Welker *et al.* 2000). As a field technique, the presence of snow fencing is less invasive than that of mesocosms and it enables a greater spatial extent of fen environments to be affected by snowpack manipulations. However, the trade-off of such an approach is that sustained alteration of surficial water levels and subsurface frost levels is unattainable due to subsurface lateral flow. In this study involving snow manipulation, lateral flow was impeded by the physical presence of the mesocosms which extended into the peat and into the surficial microhabitat of the aboveground vegetation. While this degree of artificiality compromised the maintenance of some processes that occur broadly across the fen at the scale of the mesocosm, such as subsurface hydrologic flow and evapotranspiration at the peat surface, *in situ* experiments using mesocosms represent an option to the extraction of peat monoliths for *ex situ* experimentation.

Manipulation of hydrologic properties of fens, such as surface water depth and permanence, are important for testing hypotheses involving ecological processes and evaluating water management strategies. Rates of production, respiration and decomposition, are all affected by the presence or absence of water and the aerobic conditions of the peat. To these ends, field-based mesocosms represent a novel and relatively inexpensive research technique. However, the process by which treatments were established (i.e. snow manipulations) likely inter-

ferred with desired effects on reduced frost levels with greater snow cover because of snow densification. Studies of subsurface frost dynamics as a function of increased winter snow cover are confounded with this experimental mesocosm design. The obvious solution to this problem would be to retain a high degree of snow loft in the snow addition mesocosms. Considering that any physical manipulation of snow will result in increased densification, multiple contrasts in snow cover depths beyond ambient accumulations in a field setting might only be achieved during years with high rates of snowfall or through the production of artificial snow.

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References

- Aurela M., Laurila T. & Tuovinen J.-P. 2004. The timing of snow melt controls the annual CO₂ balance in a subarctic fen. *Geophys. Res. Lett.* 31, L16119, doi:10.1029/2004GL020315.
- Bridgman S.D., Pastor J., Updegraff K., Malterer T.J., Johnson K., Harth C. & Chen J. 1999. Ecosystem controls over temperature and energy flux in northern peatlands. *Ecol. Appl.* 9: 1345–1358.
- Bubier J.L. 1995. The relationship of vegetation to methane emission and hydrochemical gradients in northern peatlands. *J. Ecol.* 83: 403–420.
- Camill P. 1999. Patterns of boreal permafrost peatland vegetation across environmental gradients sensitive to climate warming. *Can. J. Bot.* 77: 721–733.
- Carroll P. & Crill P. 1997. Carbon balance of a temperate poor fen. *Global Biogeochem. Cy.* 11: 349–356.
- Diaz H.F. 1986. An analysis of twentieth century climate fluctuations in northern North America. *J. Clim. Appl. Meteorol.* 25: 1625–1657.
- FitzGibbon J.E. 1981. Thawing of seasonally frozen ground in organic terrain in central Saskatchewan. *Can. J. Earth Sci.* 18: 1492–1496.
- Frost T.M., DeAngelis S.M., Bartell D.J., Hall D.J. & Hurlbert S.H. 1988. Scale in the design and interpretation of aquatic community research. In: Carpenter S.R. (ed.), *Complex interactions in lake communities*, Springer, New York, USA, pp. 229–258.
- Gignac L.D., Nicholson B.J. & Bayley S.E. 1998. The utilization of bryophytes in bioclimatic modeling: predicted northward migration of peatlands in the Mackenzie River Basin, Canada, as a result of global warming. *Bryologist* 101: 572–587.
- Goodrich L.E. 1982. The influence of snow cover on the ground thermal regime. *Can. Geotech. J.* 19: 421–432.
- Gorham E. 1991. Northern peatlands: Role in the carbon cycle and probable responses to global warming. *Ecol. Appl.* 1: 182–195.
- Granberg G., Grip H., Ottosson Löfvenius M., Sundh I., Svensson B.H. & Nilsson M. 1999. A simple model for simulation of water content, soil frost, and soil temperatures in boreal mixed mires. *Water Resour. Res.* 35: 3771–3782.
- Groffman P.M., Driscoll C.T., Fahey T.J., Hardy J.P., Fitzhugh R.D. & Tierney G.L. 2001. Colder soils in a warmer world: a snow manipulation study in a northern hardwood forest ecosystem. *Biogeochemistry* 56: 135–150.
- Hogan J.M. 2006. *Hydrologic behaviour and hydraulic properties of a patterned fen in Saskatchewan*. M.Sc. thesis, University of Saskatchewan, Saskatoon, Saskatchewan.
- Hogg E.H. 1997. Temporal scaling of moisture and the forest-grassland boundary in western Canada. *Agr. Forest Meteorol.* 84: 115–122.
- Johnson D., Kershaw L., MacKinnon A. & Pojar J. 1995. *Plants of the western boreal forest and aspen parkland*. Lone Pine Publishing, Edmonton, Alberta.
- Kingsbury C.M. & Moore T.R. 1987. The freeze-thaw cycle of a subarctic fen, northern Quebec. *Arctic Alpine Res.* 19: 289–295.
- Ling F. & Zhang T. 2003. Impact of the timing and duration of seasonal snow cover on the active layer and permafrost in the Alaskan arctic. *Permafrost Periglac.* 14: 141–150.
- Moore T.R. 1987. Thermal regime of peatlands in subarctic eastern Canada. *Can. J. Earth Sci.* 24: 1352–1359.
- Moore T.R. 1989. Plant production, decomposition and carbon efflux in a subarctic patterned fen. *Arctic Alpine Res.* 21: 156–162.
- Moore T.R., Roulet N.T. & Waddington J.M. 1998. Uncertainty in predicting the effect of climatic change on the carbon cycling of Canadian peatlands. *Climatic Change*. 40: 229–245.
- Nijssen B. & Lettenmaier D.P. 2002. Water balance dynamics of a boreal forest watershed: White Gull Creek Basin, 1994–1996. *Water Resour. Res.* 38: 37.1–37.12.
- Price D.T., Pen C.H., Apps M.J. & Halliwell C.H. 1999. Simulating effects of climate change on boreal ecosystem carbon pools in central Canada. *J. Biogeogr.* 26: 1237–1248.
- Quinton W.L. & Roulet N.T. 1998. Spring and summer runoff hydrology of a subarctic pattern wetland. *Arctic Alpine Res.* 30: 285–294.
- Rask H., Schoenau J. & Anderson D. 2002. Factors influencing methane flux from a boreal forest wetland in Saskatchewan, Canada. *Soil Biol. Biochem.* 34: 435–443.

- Romanovsky V.E. & Osterkamp T.E. 2000. Effects of unfrozen water on heat and mass transport processes in the active layer and permafrost. *Permafrost Periglac.* 11: 219–239.
- Scott P.A. & Rouse W.R. 1995. Impacts of increased winter snow cover on upland tundra vegetation: a case example. *Clim. Res.* 5: 25–30.
- Sturm M., Holmgren J., König M. & Morris K. 1997. The thermal conductivity of seasonal snow. *Journal of Glaciol.* 43: 26–41.
- Thormann M.N., Bayley S.E. & Szumigalski A.R. 1998. Effects of hydrologic changes on aboveground production and surface water chemistry in two boreal peatlands in Alberta: implications for global warming. *Hydrobiologia* 362: 171–183.
- Tilman D. 1998. Species composition, species diversity and ecosystem processes: understanding the impacts of global change. In: Pace M.L. & Groffman P.M. (eds.), *Successes, limitations and frontiers in ecosystem science*, Springer-Verlag, New York, pp. 452–472.
- Van der Valk A.G. 2005. Water-level fluctuations in North American prairie wetlands. *Hydrobiologia* 539: 171–188.
- Vitousek P.M. 1994. Beyond global warming: ecology and global change. *Ecology* 75: 1861–1876.
- Welker J.M., Fahnestock J.T. & Jones M.H. 2000. Annual CO₂ flux in dry and moist Arctic tundra: field responses to increases in summer temperatures and winter snow depth. *Climatic Change*. 44: 139–150.
- Weltzin J.F., Bridgham S.D., Pastor J., Chen J. & Harth C. 2003. Potential effects of warming and drying on peatland plant community composition. *Glob. Change Biol.* 9: 141–151.
- Woo M.-K. & Winter T.C. 1993. The role of permafrost and seasonal frost in the hydrology of northern wetlands in North America. *J. Hydrol.* 141: 5–31.
- Zoltai S.C., Taylor S., Jeglum J.K., Mills G.F. & Johnson J.D. 1988. *Wetlands of boreal Canada, national wetlands of Canada*. Ecological Land Classification Series No. 24. Sustainable Development Branch, Environment Canada, Ottawa, Ontario, Canada, and Polyscience Publications, Montreal, Quebec, Canada.